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Geographic Variation in *Microtus nivalis* (Martins, 1842) from Austria and Yugoslavia

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Abstract. 387 snow voles from Austria and Yugoslavia, assignated to 13 geographic samples were examined. The analyses of colour, enamel tooth pattern, external, and skull dimensions showed that not even two geographic samples are identical. The interorbital constriction and the braincase height clinally increase in the northwest—southeast direction. The geographic samples from Macedonia, Galičica mountain in particular, are the most distinct from all the others. The subspecies category is considered inadequate for describing the complex geographic variations found in the snow vole populations in Austria and Yugoslavia.

Key words. Mammalia, Arvicolidae, *Microtus nivalis*, Austria, Yugoslavia, variability, taxonomy.

Introduction

The snow vole populates mainly mountainous regions in the south of Europe, from the Pyrenees to the Balkans, Asia Minor, the Caucasus and Lebanon as far east as Iran (Corbet 1978; Krapp 1982). Its distribution is discontinuous and of a relic character. The upper Pleistocene distribution of snow voles was larger than the present one (Terzea 1972). Due to the reduction of the distribution area to mainly treeless islands with cavernicolous conditions at the end of the Pleistocene, one could expect single populations to have been isolated for approximately 10,000 years. Consequently, a considerable number of subspecies is recognized. Ellerman & Morrison-Scott (1966) listed 16 subspecies while Krapp (1982) recognized 12 in Europe. Kratochvil (1981) added six "natios" to this number. Comprehensive approaches towards the description of variability and classification on a larger geographic scale are rare. One of the first attempts is that of Spitzenberger (1971) but the most recent, as well as the most comprehensive one, is that of Kratochvil (1981).

No revision has been published recently of the actual subspecific status of snow vole populations from the southeastern Alps and Dinaric Alps. Austrian snow voles were thought to represent nominate subspecies (Wettstein-Westerheimb 1955) while three forms were reported in Yugoslavia by Djulić & Mirić (1967): *M. n. wagneri*, *M. n. malyi* and *M. n. ulpius*. The first two were described on the basis of the Yugoslav material.

The aim of the present study is to describe the geographic variability in 13 snow vole populations from the Austrian Alps and Yugoslavia, and to evaluate the validity of subspecies recognized by the previous authors.

Fig. 1: Outline of Austria and Yugoslavia showing the position and designated number of each geographic sample.

Material and Methods

387 speciemens of snow voles (381 skulls, 222 skins and 5 spirit specimens) from Austria and Yugoslavia were examined. The material is deposited in the collections of the Naturhistorisches Museum Wien (140 specimens), Slovene Museum of Natural History (130 specimens), and the collection of B. Petrov (117 specimens). According to the criteria of Kratochvil (1981), 195 specimens were adult. In addition the type of *M. nivalis malyi* (Zemaljski muzej Bosne i Hercegovine, Sarajevo) and one young topotype of this subspecies (Naturhistorisches Museum Wien) were examined.

The specimens were assigned to 13 geographic samples (Fig. 1) for analysis of morphometric variations within and among populations. Sample areas were kept as small as possible and selected so as to represent an integral geographic area. In no instance did a sample area cross any previously recognized taxonomic boundary. The total sample size of examined specimens is indicated in parentheses, it is followed by the number of adults. Sample 1 — Tauplitzalm; alt. 1550—1880 m (53/21). Sample 2 — Hohe Tauern; specific localities: Grossglockner, Pflüglhof, Franz Josefshaus, Innerkrems, Innerfragant; alt. 1700—2360 m (42/18). Sample 3 — Karnische Alps; localities: Obere Bischof-Alm, Volayerbachtal, Nassfeld, Schlanitzen; alt. 706—1573 m (45/13). Sample 4 — Julian Alps; localities: Mangart, Kanin, Polovnik, Krnsko jezero, Kredarica, Krma, Vršič, Planica; alt. 440—2450 m (56/36). Sample 5 — Northwest Dinaric Alps; localities: Snežnik, Cerkniško jezero, Hrvatski Snježnik, Risnjak; alt. 550—1700 m (32/17). Sample 6 — Velebit Mts.; localities: Zavižan, Alan, Štirovača, Prezid; alt. 800—1500 m (30/17). Sample 7 — Bosnia; localities: Cincar, Šator; alt. 1300—1700 m (16/7). Sample 8 — Durmitor; localities: Valovito jezero, Crepuljna poljana; alt. 1700 m (20/15). Sample 9 — Komovi mountain, Štavna; alt. 1750 m (20/12). Sample 10 — Šar planina mountains; localities: Popova Šapka, Titov vrh, Stojkova kuća; alt. 1900—2750 m (33/10). Sample 11 — Pelister mountain; localities: Kopanke, Golemo Ezero; alt. 1750—2250 m (9/8). Sample 12 — Galičica, alt. 1600 m (5/4). Sample 13 — East Serbia; localities: Stara planina, Suva planina Basara; alt. 1200—1900 m (27/17).

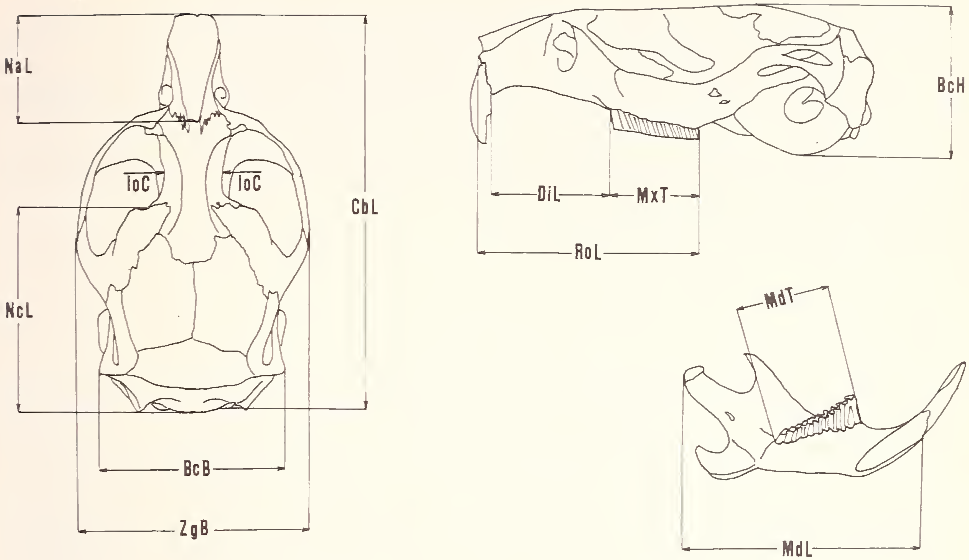

Fig. 2: Snow vole skull and mandible illustrating the parameters that were measured. See text for abbreviations.

Snow vole samples from three large mountain systems were thus analyzed, namely from the Alps (samples 1 to 4), Dinaric Alps (samples 5 to 12), and Balkan Mountains (sample 13).

Geographic variation in the colour of pelage was analysed in adults only. The terms used to describe the colour were those given by Munsell (1975). Besides adults, subadults and young specimens with developed enamel tooth pattern were also included in the analyses of molar patterns. The nomenclature by Hibbard (1950; according to Van der Meulen 1973) was adopted in the descriptions of tooth structure. The abbreviations are as follows: T — triangle, AC — anterior cup, PC — posterior cup, BSA — buccal salient angle, LSA — lingual salient angle, BRA — buccal re-entrant angle, LRA — lingual re-entrant angle. With respect to their morphology teeth were divided into groups referred to as morphotypes. Each recognized morphotype is illustrated.

External measurements were recorded from specimen labels. Their abbreviations and symbols are as follows: HB — head and body length, TL — tail length, HF — hind foot length, and E — ear length.

Twelve linear measurements were taken on each of the adult skulls using a vernier caliper with an accuracy to the nearest 0.1 mm (Fig. 2). The abbreviations used are: CbL — condylobasal length, RoL — rostrum length, NcL — length of neurocranium, NaL — nasal length, MxT — maxillary toothrow length, DiL — diastema length, MdL — mandible length, MdT — mandibular tooth row length, ZgB — zygomatic breadth, BcB — braincase breadth, IoC — interorbital constriction, BcH — braincase height per bullae.

Two quotient indices used by previous authors to distinguish subspecies of *M. nivalis* were calculated: TL x 100 : HB = IND 1, and ZgB x 100 : CbL = IND 2.

Variations in mensural characters among geographic samples were analyzed using standard and multivariate analyses. Standard statistical tests (mean and standard deviation) were applied in all comparisons involving a single quantitative character. The differences among 13 geographic samples were investigated using one-way analysis of variance. Only adults were used in the above statistical comparisons. To estimate how near one geographic sample was to

another on the basis of morphotype frequencies of molars, a method using vector algebra proposed by Cavalli-Sforza & Edwards (1967; according to Batschelet 1975) was applied.

For comparisons among geographic samples involving variations in a number of quantitative characters simultaneously, I used a principal component analysis (PCA), as described by Nie et al. (1975). Only skull measurements of adult specimens were used in the present PCA.

Cluster analyses were conducted with an unweighed pair-group method using arithmetical averages (UPGMA) on the correlation matrix.

Results

Colour

Snow voles from the Alps (samples 1, 2, 3, 4) and NW Dinaric Alps (samples 5, 6) were brown/dark brown 7.5 YR 4/2 to dark brown 7.5 YR 3/2 or grayish brown 10 YR 4/2. Towards the south-east the snow voles became paler. Bosnian animals (sample 7) were similar to the Alpine ones but were slightly paler. Durmitor snow voles (sample 8) were grayish brown 10 YR 5/2 to pale brown 10 YR 6/3. Snow voles from Komovi (sample 9) were the palest, being pale brown 10 YR 6/3 to grayish brown 10 YR 5/2. Specimens from the Šar platina mountains (sample 10) approached dark yellowish brown 10 YR 4/4. Animals from geographic samples 11 and 12 were grayish brown 10 YR 5/2 but slightly darker than those from Komovi. East Serbian snow voles (sample 13) were brown/dark brown 7.5 YR 4/2 or 7.5 YR 4/4.

The belly was light gray/gray 10 YR 6/1 in darker populations, from the Alps as far as Bosnia and Durmitor, and light gray 10 YR 7/1 or 10 YR 7/2 in paler ones. Snow voles from east Serbia (sample 13) had a light gray/gray 10 YR 6/1 to very pale brown 10 YR 7/3 belly.

The tail was indistinctly bicoloured to uniform. It was usually paler in pale populations. The colour of the upper side varied, being light gray 10 YR 8/1, pinkish gray 7.5 YR 7/2 to very pale brown 10 YR 7/3. The feet were light gray 10 YR 8/1.

In general, the snow voles from the Alps and northwestern Dinaric Alps were darker with distinct dark brown tones. Dinaric populations, starting from sample 8 in the northwest, were paler with prevailing grayish tones. This trend was best expressed in geographic sample 9 where in their colour some extreme specimens resembled *Apodemus mystacinus*. East Serbian snow voles (sample 13) approached the Alpine ones but were slightly paler with some reddish tones.

Dentition

First upper molar (M^1)

The first upper molar was most variable in its posterior end. The base of T4 could be short and broad (Fig. 3a) but was usually long and narrow (Fig. 3b); one quarter of the specimens examined had small enamel evaginations on the lingual side (Fig. 3c, d). Such complexities were not recorded in geographic samples 5, 8, 11, and 12. In sample 9 this evagination was sometimes enlarged into an additional triangle T5 which was broadly confluent with T4 (Fig. 3e). A well developed T5 was found in 4 out of 17 snow voles from sample 9. Due to these intricacies, specimens from geographic sample 9 had the relatively longest posterior part of M^1.

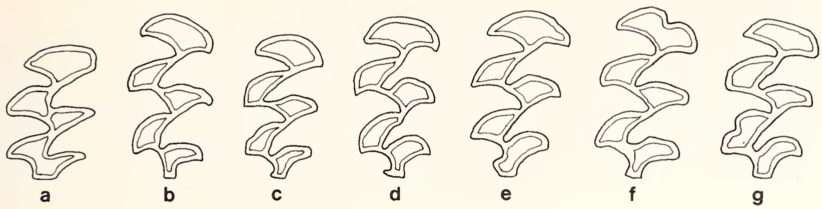

Fig. 3: Morphological variability of M^1 in *Microtus nivalis* from Austria and Yugoslavia.

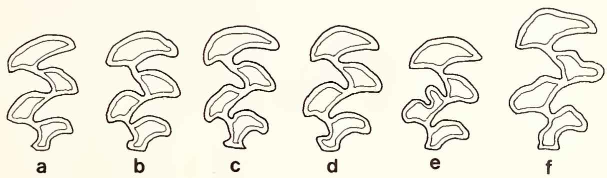

Fig. 4: Morphological variability of M^2 in *Microtus nivalis* from Austria and Yugoslavia.

A deep anteromedial groove in the anterior loop (Fig. 3f) was found in one specimen from Pelister (sample 11). A shallower sulcus was also recorded in one specimen from Snežnik (sample 5) and one from Tauplitzalm (sample 1).

In one snow vole from Tauplitzalm (sample 1) a groove was found on T3 (Fig. 3g), corresponding to the radnensis morphotype of M^2. It is worth mentioning that M^2 in this specimen was in fact of the radnensis type. A shallower groove was also observed in two specimens from geographic sample 9 and one from sample 11.

Second upper molar (M^2)

Intricacies similar to those on M^1 were observed also on the posterior part of M^2. Minor lingual evaginations of enamel at the base of T4 were observed in all examined geographic samples (Fig. 4a, b, c). A well developed additional triangle T5, always broadly confluent with T4 (Fig. 4d), was found in 7.3 % of the snow voles. It was most frequent in geographic sample 9 where it was established in 7 out of 17 specimens (41 %). T5 was not found in snow voles from samples 1, 5, 8, 11, and 12.

The radnensis morphotype (Fig. 4e) was rare, occurring in 5 snow voles (1.7 %) from samples 1, 2, 3, and 5. With the exception of one specimen from Snežnik (sample 5) the radnensis morphotype was absent in all the other Dinaric populations. Two snow voles with a shallow groove on T3 surprisingly were found again in eastern Serbia (13). One of them had a shallow groove on T2 as well (Fig. 4f).

Third upper molar (M^3)

Simplex (Fig. 5a, b) and typica (Fig. 5c, d) were the predominant morphotypes of M^3. In both can the dentine field of T4 be isolated (Fig. 5a, c) or connected with the posterior cap (Fig. 5b, d). The simplex morphotype was found in 58.1 % of voles examined (n = 284), with frequencies ranging between 20 % (geographic sample 6)

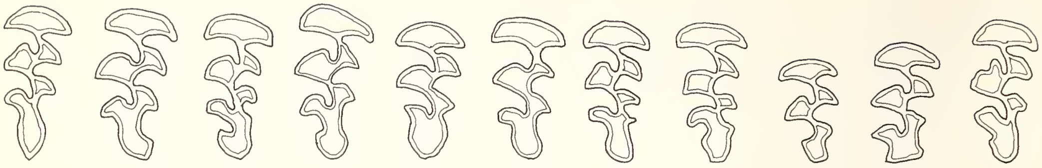

Fig. 5: Morphological variability of M³ in *Microtus nivalis* from Austria and Yugoslavia.

Table 1: Frequency of occurrence of simplex morphotype (M³) in 13 geographic samples of *M. nivalis* from Austria and Yugoslavia. Identifying numbers refer to sample areas (Fig. 1).

Sample	N	% simplex
1	30	83.3
2	25	84.0
3	26	34.6
4	53	50.9
5	22	50.0
6	25	20.0
7	12	58.3
8	19	68.4
9	17	47.1
10	20	75.0
11	8	100.0
12	5	100.0
13	22	95.5

and 100 % (samples 11 and 12). It also predominated in samples 1 and 2. Typica was common in Alpine samples (3 and 4) and the northwestern Dinaric Alps (sample 5 in particular). Towards the south the simplex morphotype again gradually began to prevail, attaining a frequency of 100 % in southern Macedonia; it was also the dominant one in eastern Serbia (sample 13) as well (Table 1).

M³ with BSAS (duplicata morphotype) was found in 9 snow voles (3.2 %) from samples 1, 3, 4, 5, 6, 7, and 9 (Fig. 5g, h).

The dental field of T4 was isolated in 76.8 % of cases. Occasionally it was connected with T3 (Fig. 5e) and through it even with T2 (Fig. 5f). A strong tendency towards the reduction of PC (Fig. 5i) was recorded in Macedonian samples (especially 12) and eastern Serbia (sample 13).

One specimen from the Karnische Alps (sample 3) showed a reduction of PC which is obviously abnormal for the species (Fig. 5j).

A groove on T3 (Fig. 5k) corresponding to the radnensis morphotype on M² was found in two snow voles from geographic sample 4.

First lower molar (M_1)

Four morphotypes could be distinguished in the structure of the anteroconid (Nadachowski 1984):

1. Gud morphotype. — BRA4 and BSA4 developed, T5 and AC confluent (Fig. 6a).

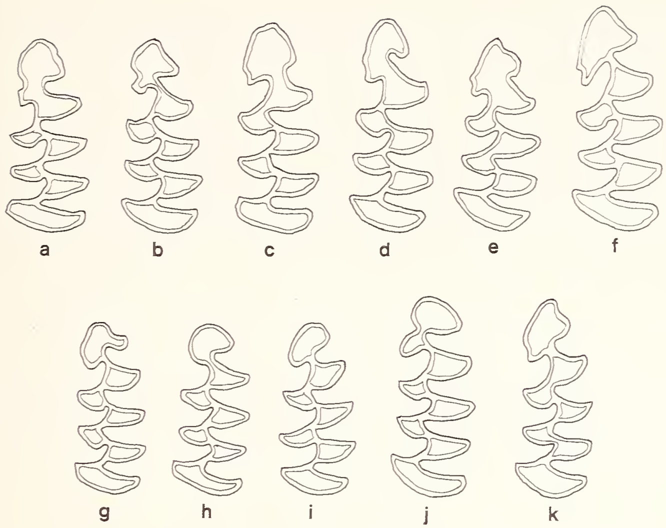

Fig. 6: Morphological variability of M_1 in *Microtus nivalis* from Austria and Yugoslavia.

Table 2: Frequency of occurrence (in %) of M_1 morphotypes in 13 geographic samples of *M. nivalis* from Austria and Yugoslavia. Identifying numbers refer to sample areas (Fig. 1.).

Sample	N	% gud	% advanced nivalid	% nivalid-ratticepid	% nivalid
1	31	0.0	3.2	64.5	32.3
2	25	0.0	4.0	28.0	68.0
3	27	3.7	0.0	33.3	63.0
4	53	3.8	7.5	17.0	71.0
5	26	3.8	15.4	15.4	65.4
6	26	3.8	0.0	23.1	73.1
7	12	0.0	8.3	0.0	91.7
8	18	22.2	11.1	44.4	22.2
9	17	5.9	5.9	17.6	70.6
10	19	0.0	0.0	31.6	68.4
11	8	0.0	0.0	25.0	75.0
12	5	0.0	0.0	40.0	60.0
13	24	0.0	16.6	16.6	66.8

This rare morphotype was present with a frequency of 3.4 % (10 specimens).

2. Advanced nivalid morphotype with retained BRA4. — Similar to gud but BRA3 deep enough to separate T5 from T6 (Fig. 6b). A rare morphotype found in 18 specimens (6.2 %).

3. Nivalid-ratticeps morphotype. — BRA4 not developed, dentine fields of T5 and T6 confluent (Fig. 6c, d, e). Present with a frequency of 27.5 % (80 specimens).

4. Typical nivalid morphotype. — T5 and T6 separated, no BRA4 (Fig. 6f, g). The most common morphotype with a frequency of 62.9 % (193 specimens).

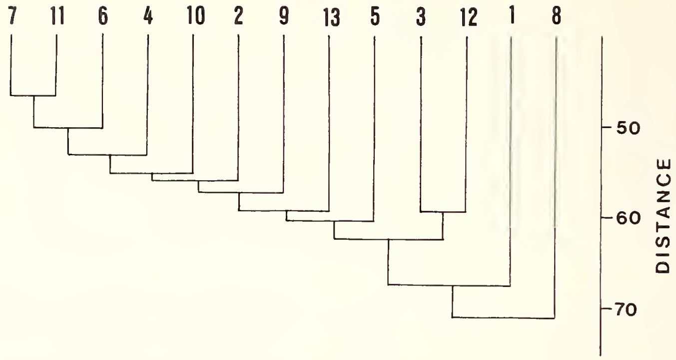

Fig. 7: Distance phenogram of *Microtus nivalis* samples produced by UPGMA clustering and based on the morphotype frequencies of the first lower molar. Identifying numbers refer to sample areas (Fig. 1).

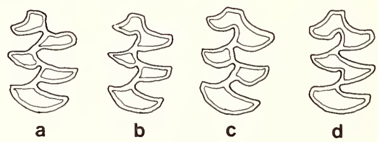

Fig. 8: Morphological variability of M_2 in *Microtus nivalis* from Austria and Yugoslavia.

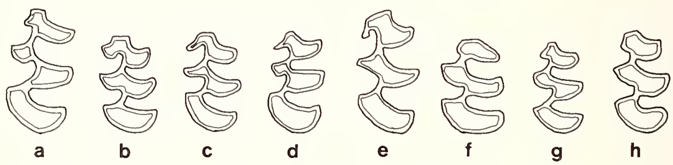

Fig. 9: Morphological variability of M_3 in *Microtus nivalis* from Austria and Yugoslavia.

The frequency of morphotypes in different geographic samples is shown in table 2. The ratticepid morphotype was not found in our material, although there were tendencies towards the reduction of BSA4 (Fig. 6h). With the exception of geographic samples 1 and 8 the nivalid morphotype was the most frequent. Populations from Macedonia (samples 10, 11, 12) obviously did not develop BRA4 at all. Sample 12 had a frequently simplified oval shaped AC (Fig. 6i). In all Bosnian specimens (sample 7) T5 and T6 were always separated.

The distance phenogram (the coefficient of cophenetic correlation was 0.891) based on the frequencies of these four morphotypes did not cluster samples on a geographic basis (Fig. 7), thus showing a chaining hierarchy. Considerable distances were found among geographic samples without any clear relations.

The following atypical morphotypes of M_1 with low frequencies are worth men-

tioning: deep BRA4 which nearly isolated T6 from AC (Fig. 6j), confluent dental fields of T4 and T5 (Fig. 6e), T1 and T2 (Fig. 6k), T3 and T4 (Fig. 6d).

Second lower molar (M_2)

Dental fields of T3 and T4 were separated (Fig. 8a) in 24.7 % of thespecimens (range from 3.1 % for sample 1 to 40.0 % for sample 6). In approximately one third (30.2 %) these triangles were broadly confluent (Fig. 8b, c). In some specimens dental fields of T1 and T2 were also confluent (Fig. 8d).

Third lower molar (M_3)

Dental fields of T3 and T4 were always confluent while those of T1 and T2 were separated (Fig. 9a) in 3.1 % of specimens. T4 was only rarely normally developed (Fig. 9b), being reduced in varying degrees in the majority of specimens. It was frequently compressed from the sides so that it was more or less narrowed (Fig. 9c). The next step was the reduction of the dental field until there remained only an enamel fold (Fig. 9d). The fold was sometimes deformed (Fig. 9e) but usually nearly (Fig. 9a) or completely reduced (Fig. 9f). Another way of reduction of T4 was a simple shortening of a normally developed triangle (Fig. 9g, h) leading to the same result. Different degrees of reduction of the dental field of T4 were a normal feature in each sample examined, being more frequent and obvious in the snow voles from the Balkan Peninsula, especially in geographic samples 9, 12, and 13. However, the overlapping was wide and consequently there were no clear-cut differences between geographic samples in this respect.

The posterior margin of the palate

The shape and structure of the posterior margin of the palate were most variable. The squama carinae mediae was usually low and ill defined or completely reduced. High squama, distinctly separated from the postero-lateral pits (Fossae palatinae laterales), was only one end of the continuous variability. So its recognition involved arbitrary categorization. In any event a high sqama was rare in the material examined, being found only in 12 % of the specimens. It had the highest frequency in geographic samples 5 and 6 where it was found in one third to nearly one half of the cases. Among the four Alpine samples (1 to 4) high sqama was rare, found in approximately 10 %. Dinaric samples from 7 to 12 had no high sqama at all. In sample 13a high squama was found again in 18 % of specimens examined (Tab. 3).

The shape of the anterior edge of the fossa interpterygoidea also varied, being straight or semicircular. In some specimens the squama carinae mediae protruded backwards (the margin had a V or W shape in such cases) or, on the other hand, did not reach the edge of the interpterigoid fossa at all.

The foramen palatinum posterior was either connected with the fossae palatinae laterales or else separated from them by a bony bridge of the os palatinum. The presence of a bony bridge showed a distinct northwest — southeast cline (Tab. 3). Rare in the Austrian Alps (samples 1 to 3), it was nearly always present in Macedonia (here sample 12 was not taken into consideration due to the small number of specimens). Geographic sample 13 in this respect corresponded to the snow voles from Montenegro (samples 8 and 9).

Table 3: The shape of squama carina media and the condition of the bony bridge between the foramen palatinum posterior and the fossae palatinae laterales in 13 geographic samples of *M. nivalis* from Austria and Yugoslavia. Intermediate cases were not included. Identifying numbers refer to sample areas (Fig. 1).

		Squama carinae mediae		Bony bridge between For. palatinum post. and Fossa palatina lat.	
Sample	N	% low	% high	% absent	% broad
1	28	71.4	3.6	17.9	21.4
2	14	57.1	0.0	35.7	21.4
3	22	50.0	9.1	40.9	22.7
4	52	65.4	9.6	40.4	32.7
5	26	3.8	46.2	26.9	30.8
6	24	37.5	33.3	41.7	41.7
7	10	60.0	0.0	10.0	40.0
8	18	72.2	0.0	5.6	55.6
9	17	70.6	0.0	11.8	70.6
10	19	63.2	0.0	5.3	94.7
11	8	75.0	0.0	100.0	0.0
12	4	100.0	0.0	0.0	50.0
13	22	36.4	18.2	0.0	68.2

Univariate analysis

All mensural characters with the exception of the braincase breadth differed significantly (at the level of $p < 0.01$ %) among the 13 geographic samples studied (Table 4). If the condylobasal length of the skull is taken as the indicator of size, large snow voles were from samples 1, 5, 7, 8, 9, and 10. The animals in sample 12 were small with the average condylobasal length approaching minimal values of the remaining snow vole samples.

In order to study general trends in snow vole morphology, correlation coefficients (r) were calculated between the character means and the latitude. Geographic sample 13 was excluded from this analysis, since it belongs to a mountain system other than the Alps or Dinaric Alps. Thus, possible clines along the northwest — southeast axis were obtained. Out of 16 mensural characters examined only interorbital constriction and braincase height per bullae differed significantly from zero at the $P < 0.05$ % level, having r values of —0.658 and —0.647 respectively. Both these characters were thus on the increase towards the southeast. All of the other measurements revealed no simple pattern of geographic variation.

Of the quotient indices, relative tail length (IND 1) differed significantly among the 13 geographic samples. The long-tailed snow voles were from sample 1, while relatively short-tailed animals were found in samples 7 and 11. However, since HB and TL were measured by different collectors using different methods (TL was measured either from the anus or the sacral vertebrae), variation of IND 1 was influenced also by differences in measurement techniques.

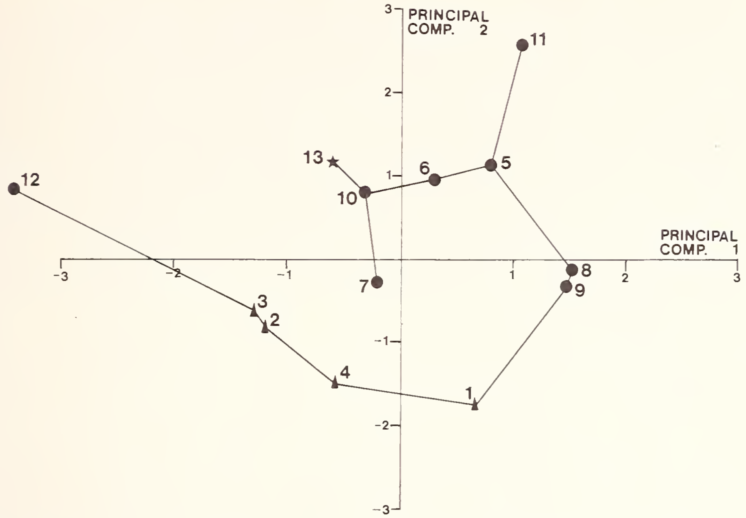

Fig. 10: Projections of 13 samples of Austrian and Yugoslavian *Microtus nivalis* onto the first two principal components. Identifying numbers refer to sample areas (Fig. 1). Triangles — Alpine samples; dots — Dinaric samples; star — east Serbian sample.

The relative braincase breadth (IND 2) showed no significant interpopulation variability. Since IND 2 broadly describes the skull shape, we can conclude from the results of univariate analysis that shape is less variable between samples than the size.

Multivariate analysis

Results from 13-sample principal component analysis are given in the plot of projections of sample onto the first two principal components (Fig. 10). Size related characters are generally more important in determining the first principal component (Lemen 1983), and this is well obvious also from character loadings of the interlocality variation in our snow vole samples. Length characters (CbL, RoL, DiL) contributed most to the first principal component by high positive values, while IoC has a high negative loading for this component. Interorbital constriction is usually negatively correlated with age and size in voles, thus the smaller the interorbital constriction, the larger the vole. Sample 12 had high negative loadings for the first principal component, and consequently snow voles from Galičica would be expected to be the smallest. This corresponds well with the results of univariate analyses. High positive values of the first principal component were found in geographic samples 1, 5, 6, 8, 9, and 11 which means that they are the largest. Samples 2, 3, 4, 7, 10, and 13 appeared to be intermediate in size. The second principal component is interpreted as an indicator of shape similarity (Lemen 1983) i. e. the smaller the distance between geographic samples, the greater the shape similarity. In our results IoC and BcH contributed most to the second principal component by positive loadings and

DiL by a negative one. Sample 11 had high positive loadings for the second principal component, i. e. its skull shape was the most unique of all. The Alpine samples (1 to 4) clustered well together having high negative loadings for the second principal component. Snow voles from the Alps tended to be more similar in shape than in size. The samples from the Dinaric Alps (with the exception of sample 11) were more similar to sample 13 than to the Alpine ones. It can be concluded that snow vole samples clustered better geographically according to shape than according to size. Shape delimited the Alpine samples on one hand from the Dinaric ones on the other. The Pelister sample (11) differed in shape from all of them. Sample 12, which was characterized by a small size (low values for the first principal component) approached the Dinaric samples in shape.

Results of the cluster analysis, performed from the distance matrix for the first two principal components, are depicted as a phenogram in fig. 11. The coefficient of cophenetic correlation was 0.807. Three Alpine samples (2 to 4) clustered together, while sample 1 appeared to be closer to the Montenegrin snow voles (samples 8 and 9). The Dinaric snow vole samples could not be arranged into one cluster, which means that they are not phenetically close. The snow voles from the southern Dinaric Alps (samples 11 and 12) differed from all other samples, showing neither similarity to them nor to one another.

Table 4: Means and standard deviations of metrical characteristics (in mm) and quotient indices for each of the 13 geographic samples of *Microtus nivalis* from Austria and Yugoslavia referenced in fig. 1. See text for abbreviations. Statistical significance: * P <0.01, n. s. = not significant.

Sample	HB	TL	HF	E	CbL	RoL	NcL	NaL	MxT
1	122.4±4.91	60.2±3.12	19.71±0.49	17.87±2.07	29.72±0.71	17.83±0.34	16.19±0.49	8.11±0.25	7.19±0.20
2	118.5±5.81	62.3±5.39	18.58±1.72	16.75±1.48	28.71±0.39	17.22±0.31	15.51±0.26	8.00±0.33	7.10±0.32
3	114.3±3.60	72.8±3.00	19.58±0.65	15.91±0.64	28.55±1.08	17.32±0.48	15.72±0.50	8.05±0.44	7.08±0.32
4	126.0±4.31	69.5±4.62	20.77±0.90	14.67±0.85	29.04±0.86	17.66±0.53	15.64±0.52	7.91±0.38	7.12±0.27
5	132.6±6.36	66.3±4.37	21.35±0.63	14.49±0.78	30.22±0.82	18.34±0.57	16.35±0.51	8.32±0.32	7.49±0.26
6	126.8±5.49	63.3±3.79	21.13±0.97	13.83±0.79	29.48±0.88	18.00±0.62	16.13±0.45	8.19±0.38	7.49±0.30
7	129.7±4.75	62.0±6.35	21.19±1.05	14.43±0.83	29.58±0.34	17.98±0.37	15.75±0.28	8.20±0.22	7.45±0.24
8	130.0±4.69	68.4±4.16	20.59±0.76	15.59±0.80	29.94±0.53	18.23±0.39	16.29±0.33	8.23±0.40	7.47±0.22
9	127.3±3.29	69.6±3.01	20.74±0.50	15.69±0.44	29.87±0.60	18.28±0.35	16.05±0.42	8.43±0.27	7.38±0.21
10	126.5±5.32	62.9±5.69	20.22±0.84	15.09±0.56	29.26±0.49	17.78±0.51	15.94±0.40	7.93±0.31	7.26±0.33
11	135.8±5.60	61.6±4.69	20.81±0.60	15.74±0.82	29.98±1.11	18.25±0.70	16.44±0.57	8.50±0.60	7.54±0.35
12	120.2±3.90	59.6±1.14	19.96±0.80	15.00±1.93	28.04±1.24	16.94±0.83	15.14±0.36	7.66±0.36	7.02±0.46
13	126.4±6.25	67.5±4.95	21.16±0.62	14.76±0.84	29.27±0.88	17.56±0.66	16.15±0.45	8.36±0.42	7.36±0.30
F-test	15.61*	12.25*	12.03*	16.82*	5.97*	8.56*	6.87*	4.35*	6.62*

Sample	DiL	MdL	MdT	ZgB	BcB	IoC	BcH	IND 1	IND 2
1	8.60±0.26	17.73±0.51	6.99±0.17	16.85±0.45	14.24±0.38	4.11±0.17	8.66±0.34	49.00±3.24	56.32±1.50
2	8.31±0.25	17.37±0.32	6.96±0.22	16.50±0.31	14.00±0.41	4.22±0.23	8.65±0.27	52.37±5.88	57.66±1.18
3	8.38±0.27	17.73±3.07	6.80±0.27	16.48±0.55	13.88±0.70	4.19±0.14	8.60±0.25	63.90±3.69	57.83±1.37
4	8.68±0.31	17.37±0.59	6.81±0.21	16.68±0.55	13.91±0.49	4.25±0.18	8.48±0.26	55.11±3.34	57.41±1.25
5	8.85±0.32	18.46±0.49	7.27±0.36	17.06±0.56	14.20±0.38	4.48±0.16	9.13±0.43	49.96±3.41	56.48±1.26
6	8.62±0.31	18.30±0.68	7.15±0.23	16.71±0.65	14.08±0.56	4.40±0.14	8.93±0.30	49.89±1.76	56.66±1.24
7	8.42±0.15	18.17±0.32	7.13±0.23	17.25±0.27	14.23±0.30	4.33±0.19	8.96±0.24	47.78±4.45	58.32±0.86
8	8.83±0.32	18.23±0.42	7.19±0.25	17.07±0.41	14.24±0.34	4.26±0.14	8.99±0.34	52.02±3.34	57.03±1.28
9	8.91±0.26	18.45±0.52	7.18±0.15	17.21±0.44	14.21±0.41	4.30±0.16	9.08±0.27	54.91±3.12	57.62±1.03
10	8.72±0.33	18.01±0.51	7.10±0.25	16.63±0.54	14.11±0.31	4.47±0.11	8.83±0.18	50.29±3.29	56.76±1.42
11	8.71±0.44	18.76±0.71	7.24±0.31	17.30±0.60	14.16±0.32	4.63±0.15	9.14±0.29	45.81±2.84	57.72±1.27
12	8.06±0.38	17.42±0.58	6.54±0.34	16.00±0.91	13.36±0.34	4.32±0.13	8.86±0.42	49.93±2.52	56.63±1.39
13	8.33±0.35	17.96±0.72	6.89±0.28	16.69±0.49	13.91±0.51	4.37±0.15	8.94±0.34	53.26±3.93	57.25±0.90
F-test	7.83*	10.28*	8.95*	3.75*	2.38 n.s.	8.21*	7.86*	17.72*	2.34 n.s.

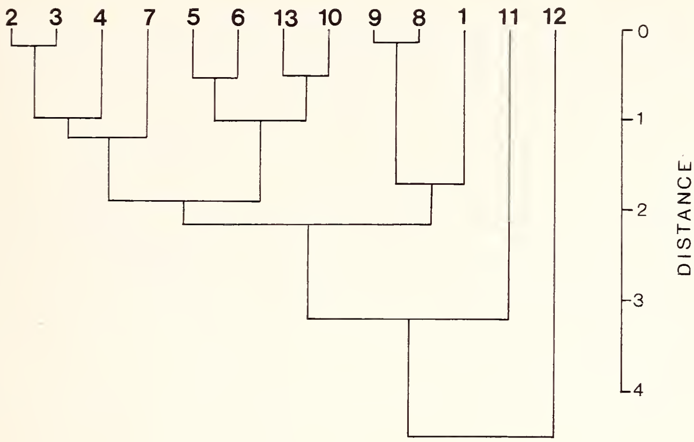

Fig. 11: UPGMA dendrogram summarizing the phenetic relationships among 13 samples of *Microtus nivalis* from Austria and Yugoslavia. Phenetic distances were obtained from the plot projections of samples onto the first two principal components. Identifying numbers refer to sample areas (Fig. 1).

Remarks on *Microtus nivalis malyi* Bolkay, 1925

The oldest name for the snow voles from the Balkans is *M. n. malyi*, described from the Tisovica valley, Prenj Mt., Herzegovina. The type is kept in the Zemaljski muzej SR Bosne i Hercegovine in Sarajevo under the number 239. The type specimen, probably male, is represented only by a skull which is damaged in the interorbital region, the base of the neurocranium and the posterior part of the left zygoma. Its measurements are as follows (in mm): CbL approx. 29.1, RoL 17.8, NcL 16.7, NaL 8.0, MxT 7.4, DiL 7.4, MdL 18.1, MdT 6.6, ZgB 16.8, BcB 14.5, IoC damaged, BcH 10.9.

The dentition showed no peculiarities. M^1 and M^2 were without evaginations on the lingual side of T4. M^3 was of the simplex morphotype with an isolated T4. M_1 belonged to the typical nivalid morphotype with a simplified oval AC. On M_2 the dental fileds of T3 and T4 were separated. T4 of M_3 was reduced (as in fig. 9f).

The squama carinae mediae was nearly completely reduced. The foramen palatinum posterior was separated from the postero-lateral pits by a bony bridge of the os palatinum.

As already mentioned, none of the characters examined showed any peculiarities not found in other Dinaric samples. Moreover, molar morphotypes and the shape of the posterior margin of the palate found in the type of *M. n. malyi* were also the most common in the remaining Dinaric snow voles. On the basis of these characters it is not possible to draw any conclusion as to which neighbouring geographic sample (6 or 7) the type resembled more closely.

The holotype was collected in 1924; obviously no further snow voles have been found on Prenj mountain. For example, on the rocky habitats in Prenj Mt. the author obtained only *Dinaromys bogdanovi*. In the Naturhistorisches Museum Wien

one young female is kept, collected in Prej in July 1901 by Arnold Penther (NMW 28169). It is preserved in alcohol but the skull has been removed. Unfortunately, the specimen is too young (W 14 grams, CbL 23.1 mm) to be of use for taxonomic purposes.

Discussion

Results of geographic variation among 13 geographic samples are briefly summarized in fig. 12. Colour (dark vs. pale) and characteristic dental morphotypes are designated. The dark morphotype is characteristic of snow vole samples in the northern part of the study area. Going towards the south-east, the pale morphotype begins to predominate with intermediates in samples 7, 8, and 13. Similar relations were observed in the distribution of the colour types in the forest dormouse (*Dryomys nitedula*) in Yugoslavia (Kryštufek 1985). Dark specimens were found in the Alps and the northwestern Dinaric Alps, corresponding to the area from which snow vole samples 4 to 6 originated. Reddish-brown forest dormice were found in Macedonia, while both colour types were collected in the intermediate area, corresponding to the area from which snow vole samples 7 to 9 originated. The adaptive significance of the dorsal pelage matching the colour of the substrate is well documented in rodents (e. g. Kaufmann 1974), but in snow voles there is apparently no connection between the substrate and the colour morphotype living on it. Thus, on white limestone both dark (as sample 4) and pale (as sample 9) morphotypes were found. On the other hand, dark metamorphic and igneous rocks on Pelister Mt. are populated by pale snow voles (sample 11). The prevailing of the pale morphotype towards the south-east could be connected with the increasing aridity in the same direction.

The localities in fig. 12 are connected by a Gabriel network (Sokal & Oden 1978). Phenetic distances obtained from the plot of projections of samples onto the first two principal components (Fig. 10) are given for the contiguous samples. Six "zones of rapid morphological change" (arbitrarily chosen phenetic distance above 2.000) can be noticed between sample pairs 1—2, 4—5, 9—10, 10—11, 10—12, and 11—12. Groups of samples within such zones were phenetically relatively close. As can be seen from fig. 10, samples 2, 3, and 4 were plotted close together, forming a relatively homogenous Alpine group of samples. Sample 1 differed in this respect from the rest of the Alpine ones. The same was true of the Dinaric samples from 5 to 9. The east Serbian snow voles (sample 13) were close to the Dinaric sample 10. The snow voles from southern Macedonia (samples 11 and in particular 12) were phenetically very peculiar. On the other hand, these "zones of rapid morphological change" did not correspond with the distribution of colour morphotypes. Such discordance between variability of pelage and mensural characters has been reported in other rodents as well (e. g. in *Onychromys leucogaster*, Engstrom & Choate 1979).

Besides colour, three characters displayed discrete northwest — southeast clines, namely IoC, BcH and the presence of a bony bridge on the os palatinum. IoC was found to depend on climatological conditions in *Microtus pennsylvanicus*, being narrower in areas with low minimum temperatures (Snell & Cunnison 1983). In the study area the average annual temperature showed no increase along the same transect as the IoC of snow voles did.

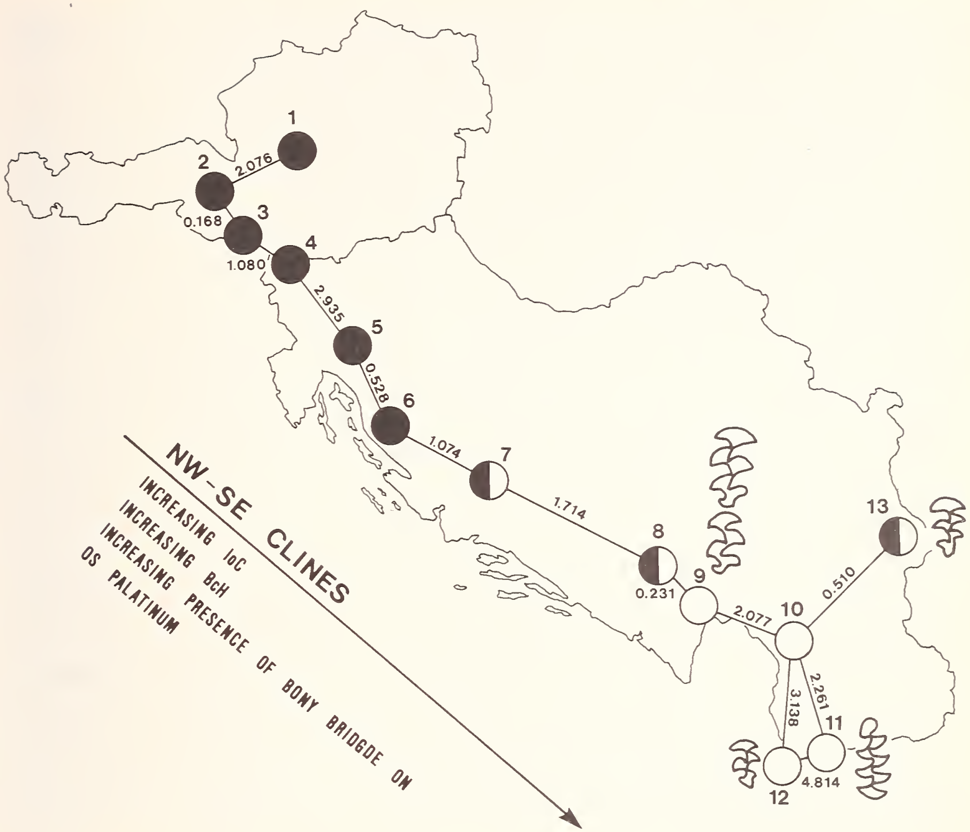

Fig. 12: Summary of the geographic variation among 13 samples of the snow vole from Austria and Yugoslavia. Distribution of colour morphotypes is designated by closed (dark morphotype) vs. open circles (pale morphotype). Half closed circles indicate intermediate morphotypes. Samples are connected by a Gabriel network and the phenetic distances from the plot projections of samples onto the first two pricipal components are given for the contiguous samples. Some characteristic dental morphotypes are denoted.

There are two main causes of geographic variations in animals, namely the limitations of the gene flow between spatially separated populations and the response of an organism to different environments (Lane & Marshall 1981). Thirteen geographic samples elaborated in this study are separated by habitats unsuitable for them. Since no gene flow can be expected, each population should be regarded as a separate evolutionary entity. It has been suggested that the snow vole is a petricolic animal, adapted to cavernicolous habitats (Kryštufek & Kovačić 1989). Such a habitat is characterized by stable, mainly stenothermal conditions. Consequently, the homeostatic stability of the morphotype would be expected in the samples studied. However, nearly all studied characters were variable in the 13 samples, and the colour and two skull dimensions showed clinal variability. In the case of colour the humidi-

ty could be responsible for its variability. Consequently, in spite of relatively stable micro-environments, a response to macro-environmental conditions could be observed among 13 geographic samples from Austria and Yugoslavia.

Morphometrical differences among samples were relatively small and only of an average character. Only sample 12 was clearly distinct from the remaining snow voles, being small in size. This population is also of interest since snow voles from the nearest allied sample (11) differed significantly in size. These two samples are approximately 20 km apart, being separated only by Prespa Lake. There are, however, considerable differences in ecological conditions between the two environments. Galičica Mt. (sample 12) is of lime stone, while Pelister Mt. (sample 11) is of metamorphic and igneous rocks. Pelister Mt. is populated by only one petricolic rodent, the snow vole, while two petricolic species, *Dinaromys bogdanovi* and *Apodemus mystacinus*, live on Galičica besides the snow vole. It is worth mentioning that *Dinaromys bogdanovi* from Galičica Mt. is also characterized by small dimensions. The condylobasal length of the adult skulls is 31.8 to 32.3 mm (3 specimens in the Slovene Museum of Natural History) while the range for the species is 31.6—34.6 mm (Petrov & Todorović). Such a decrease in the size of two petricolic voles, competing for the same habitat, could be ascribed to extreme environmental conditions, especially drought, in Galičica and the scarcity of suitable microhabitats. The latter is even more obvious through scramble competition among three petricolic rodents for the same habitat. Interesting parallelism can be observed between snow vole sample 12 and *Microtus nivalis lebrunii* (Crespon, 1844) from the southwestern Alps, a "region of unusually high summer temperature" (Miller 1912). Both animals are small (CbL in *M. n. lebrunii* less than 28 mm), both are pale and both tend towards the reduction of PC on M^3, which in *M. n. lebrunii* is also "invariably short and broad, not showing any tendency to the elongation occasionally occurring in *M. nivalis*" (Miller 1912).

The principal component analysis clustered a part of the samples according to their geographic proximity. However, it was not possible to place the results of PCA in accordance with the actual subspecific division of the snow voles in Austria and Yugoslavia. Austrian snow voles, considered to represent the nominal subspecies (Wettstein-Westerheimb 1955), are in fact not homogenous. The Tauplitzalm sample (1) was relatively distant from samples 2 and 3, which were closer to the snow voles from the Julian Alps (sample 4). The last sample is topotypical with *M. n. wagneri*, which is usually recognized to be subspecifically distinct from *M. n. nivalis* (Djulić & Mirić 1967; krapp 1982). The characters mentioned by Martino (1940) as diagnostic for *wagneri* concern the shape of AC of M_1, the PC of M^3, and IoC "which is about 4 mm . . .". Dental morphotypes cannot be regarded to be characteristic since they were found in other geographic samples as well, while IoC showed clinal variability in size with the lowest values in the northwestern part of the study area.

The Dinaric samples (5 to 12) cannot be classified as a single subspecies, i. e. *M. n. malyi*, as is usually done (e. g. Djulić & Mirić 1967) because of relatively great differences among them. Snow voles from east Serbia (sample 13) are regarded as *M. n. ulpius* (Djulić & Mirić 1967). As a matter of fact they are close to Dinaric samples, especially 5, 6, and 10. The differences between the east Serbian and Dinaric samples

contiguous to it are smaller than among the 8 Dinaric samples. Consequently, there seems to be no reason for a taxonomic separation of Dinaric snow voles from east Serbian ones. Characters proposed by Mirić (1970) to separate snow vole subspecies inhabiting Yugoslavia concern the colour of pelage and tail and the relationship between lateral fossae and the squama carinae media. The latter character showed considerable individual variability and cannot be used in the taxonomic evaluation. Colour varied from one sample to another but it was not coordinated with other characteristics of morphological variability. The fact that independent characters do not tend to be coordinated in their geographic variability, obvious from the present results, is one of the most serious limitations in applying the subspecies concept. The different characters used in this study were not in exact geographical concordance. Consequently, the greater the number of characters taken into consideration, the greater will be the total discordance and the number of races recognized (Wilson & Brown 1953). Snow vole populations are restricted to isolated stony habitats mainly on mountain tops and the subspecies concept is more easily applied on such truly distinctive populations (Edwards 1954). Such geographical fractions of the species could be defined as distinct subspecies (Wilson & Brown 1953). However, practical problems arise in applying this concept. In this study I tried to aviod the "necessary arbitrariness of any degree of population divergence chosen as the lowest formal racial level" (Wilson & Brown 1953) by recognizing the so-called "zones of rapid morphological change". However, the homogeneity was quite low within the geographic samples limited by such zones.

Kratochvil (1981) recognized 21 geographic races (subspecies and natio-s) of snow voles by a combination of relative zygomatic breadth and relative tail length. If our results from table 4 are plotted on his diagram (Fig. 17 on page 55 in Kratochvil 1981) approximately 10 races can be recognized, some 7 of them should be described and named as new ones. Inclusion of other characters into the analysis would only increase the number of races. Finally, nearly each geographical population would bring its own subspecific name. Recognized races would then be poorly determined by diagnostic characters and consequently they would be difficult to distinguish from each other. I therefore believe that the subspecies category is inadequate for describing the complex geographic variations found in the snow vole populations in Austria and Yugoslavia.

It has already been mentioned that snow vole populations with an insular distribution represent separate evolutionary entities. Since the Pleistocene distribution of snow voles was larger than the present one (Terzea 1972), the gene flow between these "evolutionary entities", has obviously been absent for some 10,000 years. There is no evidence, however, that these isolated demes developed mechanisms of reproductive isolation. Namely, the karyotypes described for most of the mountain systems in Europe populated by the snow vole, show no significant variability (Zima & Kral 1984). It is evident that speciation was slower, at least as far as can be concluded on the basis of chromosomal evolution, than in some other small mammals with a similar insular distribution. The insular distribution of the *Microspalax* complex (Savić 1982), for example probably also results from the reduction of its steppe habitat since the end of the Pleistocene. The history and the duration of geographic isolation was approximately the same in both small mammals. However, in

Microspalax this isolation produced a number of allopatric "chromosomal species" while it obviously did not result in reproductive isolation among similarly allopatric snow vole entities.

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Zusammenfassung

Es wurden 387 Schneemäuse in Österreich und Jugoslawien untersucht, welche in 13 geographische Stichproben eingeteilt wurden. Die Analyse der Farbe, der Molaren-Schmelzschlingenmuster, Körper- und Schädelmaße ergab, daß nicht einmal zwei geographische Stichproben identisch sind. Die Interorbitalbreite und Schädelhöhe vergrößern sich klinal in Richtung Nordwesten—Südosten. Die Proben aus Makedonien, vor allem vom Gebirge Galičica, unterscheiden sich am meisten von den übrigen Populationen. Die Unterartkategorie ist nicht geeignet zur Beschreibung der komplexen geographischen Variabilität, welche bei den Schneemauspopulationen aus Österreich und Jugoslawien gefunden wurde.

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